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n generations of each particular type of mating. We have the following values, where n denotes the number of ancestral generations concerned, or, as Jennings puts it, the number of successive inbreedings which have taken place.

Type of Mating	Coefficient of Inbreeding
Self-fertilization	$\frac{2^n - 1}{2^n}$
Brother \times sister	$\frac{2^n - 2}{2^n}$
Cousin \times cousin, single	$\frac{2^n - 2n}{2^n}$
Cousin \times cousin, double	$\frac{2^n - 2^2}{2^n} \begin{cases} \text{from } n=2 \\ \text{to } n=\infty \end{cases}$
Parent \times offspring	$\frac{2^n - n - 1}{2^n}$
Uncle \times niece	$\frac{2^n - 2n}{2^n}$

RAYMOND PEARL

AN ATTEMPT TO PRODUCE MUTATIONS THROUGH HYBRIDIZATION

THERE is no more interesting problem to the experimental evolutionist than the one relating to the cause or causes of the origin of mutations. Until we are able to solve this problem we can only accept what the gods give in our breeding experiments. When a mutation arises it is usually a simple process to produce a pure stock. By mutation is meant any deviation from the normal type which reappears in some of the descendants. In the following experiment most of the abnormalities that were found never reappeared in the offspring.

My experiments have been confined to the fruit fly, *Drosophila ampelophila*, a species kept for years "under cultivation" at Columbia University. This species has proved to be very plastic, throwing off great numbers of mutant forms. At the suggestion of Dr. T. H. Morgan I crossed some of these mutants with wild stock of the same species from widely separated localities in order to test whether through hybridization mutations arise in greater numbers than in inbred stock.

The idea that new forms arise from crossing more or less closely related species is an old one. One finds many references in Darwin's works to this conception. For instance, in the "Origin of Species" Darwin says:

When mongrels and the more fertile hybrids are propagated for several generations, an extreme amount of variability in the offspring in both cases is notorious; but some few instances of both hybrids and mongrels long retaining a uniform character could be given. The variability, however, in the successive generations of mongrels is, perhaps, greater than in hybrids.

One of the causes of ordinary variability . . . is . . . that the reproductive system from being eminently sensitive to changed conditions of life, fails under these circumstances to perform its proper function of producing offspring closely similar in all respects to the parent form.

From "Plants and Animals under Domestication" we find the following.

Crossing, like any other change in the conditions of life, seems to be an element, probably a potent one, in causing variability.

A variation to be effective in species formation must reappear in some of the descendants. That a variation could, through selection within a *pure strain* be increased or decreased in the direction of selection to form a stable species has been seriously questioned since Johannsen's classic experiments. It is well understood, on the other hand, how selection in a *mixed population* could cause the variation to move in the direction of selection up to a certain point.

The first mutant stock selected for the experiment was cherry club vermilion. The factors for these three characters are linked together and are also linked with sex; the second stock was black pink bent, which has the three factors independent of each other and none is linked with sex. These factors are supposed to lie in the second, third and fourth chromosomes, respectively. The third stock was black purple vestigial arc speck, which has the five factors linked together. They lie in the second chromosome. A stock from France was crossed to the mutant stock several months after the other crosses were made, and eosin tan vermilion was substituted for the cherry club vermilion, and pink kidney sooty rough for the black purple vestigial arc speck stock because flies of these particular stocks were not to be had at the time desired.

These forms were chosen because it was thought that if mutations do arise from hybrid forms there would be more probability of their origin from a mutant varying in several characters when crossed to wild than if it varied in only one character. Also by using stock containing several recessive characters a check could

be placed upon any variant from the expected classes due to contamination; for the variant, if arising from the cross, would give some offspring in the F_2 generation with some of the recessive characters. However, extreme care was taken to avoid contamination and at no time was there reason to suspect it in any of the cultures.

The wild stocks used were from Arkansas, California, Massachusetts, Illinois, Minnesota, Ohio, Wyoming, Porto Rico, Cuba, Australia and France. The totals of the F_2 generations are as follows:

	Ch. Cl. Ver.	Bl. Pk. B.	Bl. P. Vg. Arc. Sp.
Arkansas	1,162	307	198
California	859	715	332
Illinois	211		287
Massachusetts	1,078	681	1,013
Minnesota	771	274	
Ohio	506	1,612	370
Wyoming	925	150	
Porto Rico	151	207	
Cuba			819
Australia	469	401	548
France	814	951	826
Total	6,946	5,298	4,393

This gives a grand total of 16,637 flies. It should be noted that these flies were examined with the greatest care under a binocular microscope. Each fly was turned over separately and every part carefully examined.

From the cherry club vermilion crosses the following abnormal forms were found; three gynandromorphs; twenty-four flies with more or less beaded wings; two flies with three cross veins on the wings; one truncate; and two flies with abnormal abdomen.

The abnormal forms from the crosses with black purple vestigial arc speck were, sixty-three with more or less beaded wings; one truncate; one abnormal abdomen; one fly with five legs; and four flies with a projection from the posterior cross vein toward the base of the wing.

From the black pink bent crosses were found two beaded; one abnormal abdomen; three truncate; and one called furrowed because of the furrows in the eyes due to the foreshortening of the head.

This gives a total of 109 abnormal forms or one abnormal in

every 152 flies. But 89 of these abnormals were flies with beaded wings. This character is very variable; some of the flies had only a few bristles missing from the margin of the wings, while others had both the outer and inner margins of the wings serrated. The character has been recurring in the stock so frequently that it can scarcely be ascribed to outcrossing. Many of these flies were mated, but they either did not leave offspring, or the character did not reappear in the F_2 generation.

The three gynandromorphs are not to be considered as mutants. The data here show that gynandromorphs occur once in about five thousand five hundred times.

Flies with truncate wings are of occasional occurrence in the laboratory stock, as are also those with abnormal abdomen; hence, flies with these characters are not to be considered as due necessarily to the outcrossing. The truncate would not breed and the abnormal abdomen character did not reappear in the F_2 generation. If a character does not reappear in the F_2 generation it is considered to be of somatic and not of germinal origin, unless an environmental condition is necessary for the expression of the changed character.

The abnormality of the fly with five legs may have been the result of accident, for the character did not reappear in the F_2 generation.

Three characters were found to be inherited; the one called "furrowed," which arose from the cross of black pink bent with wild stock from Massachusetts; the one with a projection from the posterior cross vein toward the base of the wing, called "tau," which arose from the cross of black purple vestigial are speck with wild stock from Illinois; but since this stock had just been received from Illinois, and since the character appeared in four of the flies, it is suspected that the character was recessive in the wild stock and not due solely to the cross. Also from cherry club vermilion crossed to stock from Arkansas arose two males with three cross veins on the wings and a disturbance of the ommatidia of the eye. This character is called "warty."

Pure stocks of flies with these characters have been bred for many generations and each continues to breed true. "Warty" has many other characters than the modification of the eyes, *e. g.*, beaded wing, spread wing, from two to five cross veins on the wings, abnormal abdomen and disarranged hairs on the thorax. The females are sterile and the race is maintained

by crossing the males to their heterozygous sisters. The character is not sex linked; it decreases the viability of the flies, but more than this can not be said at present. Work is being continued on this character and on flies with the character "tau."

"Furrowed" is characterized by having the head foreshortened, which causes indentations or furrows in the eyes; also the spines on the scutellum are stumpy. The last character is of importance in determining some of the flies, as a female will sometimes occur without any disturbance of the eyes.

This character arose in a male which was crossed to a wild female. The F_2 generation gave normal females and half the males were normal and half were furrowed. This established the fact that the character followed the distribution of the sex chromosome. The position of the gene in the chromosome was next determined according to the theory that the genes in any chromosome are arranged in a linear series.¹ Crosses were made with eosin miniature, sable forked, and with vermilion barred. Because of the low fertility of the furrowed females the cross was always made with the furrowed males. Consequently, the males alone are considered in the counts given below.

EOSIN MINIATURE ♀ BY FURROWED ♂

F_2 males..	{	Normal	3	Furrowed	67
		Eosin miniature furrowed.	1	Eosin miniature	75
		Eosin long	3	Miniature	31
		Miniature furrowed	0	Eosin long furrowed	28

In the first column are the cross-over classes between miniature and furrowed and the per cent. of these to the whole number is 3.4. Then the gene which determines the character "furrowed" is supposed to lie 3.4 points beyond miniature, or at 39.6.

SABLE FORKED ♀ BY FURROWED ♂

F_2 males..	{	Furrowed sable forked...	1	Sable forked	61
		Normal	8	Furrowed	105
		Forked	3	Furrowed forked	15
		Furrowed sable	0	Sable	16

In the first column are the cross-over classes between furrowed and sable and these are 5.7 per cent. of the entire number. Then furrowed lies at a point 5.7 to the left of sable, or at 37.3.

¹ Sturtevant, *Jour. Ex. Zool.*, '13.

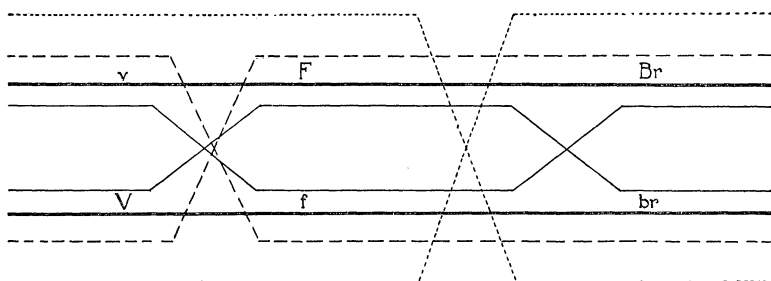
VERMILION BARRED ♀ BY FURROWED ♂

F ₂ males..	{ Bar	6	Vermilion bar.....	86
	{ Vermilion furrowed	3	Furrowed	102
	{ Normal	0	Furrowed bar.....	15
	{ Vermilion furrowed bar...	0	Vermilion	28

The cross-over classes between vermilion and furrowed are the bar and vermilion furrowed classes of which there are nine, which is 3.75 per cent. of the entire number. Vermilion is at 33, hence the gene for furrowed lies at 36.75.

The cross-over classes between furrowed and bar are the furrowed bar and the vermilion classes of which there are 43 which is 18 per cent. Then furrowed lies 18 points to the left of bar or at 39.

The discrepancy in these results is due to the low viability of the furrowed flies, yet the results agree fairly well, varying from 36.75 to 39, giving an average of 38.1, which is considered as the relative position of the gene for furrowed in the sex chromosome.



The accompanying diagram will aid in understanding the cross-over classes. The heavy straight lines represent the paired sex chromosomes which a heterozygous female has received from her parents. The upper one, which carries vermilion bar, was received from the female parent and the lower, carrying furrowed, was received from the male parent. Each of the sons of this heterozygous female receives one of these chromosomes which determines what it shall be with reference to these special characters. In about 75 per cent. of the cases the sons receive these chromosomes without any interchange of substance between the two as is shown by the two straight lines which represent the non-cross-over classes. When there is an interchange

of material between the two chromosomes as indicated by the crossed lines, then males arise with a different arrangement of the characters from that which had appeared in the grandparents.

In the diagram v, f and Br stand for vermilion eye, furrowed eye, and bar eye, respectively; while V, F and br stand for the normal allelomorphs of these characters, *i. e.*, red eye, not furrowed and not bar. Reading from the left the top dotted line includes v, F and br, but since F and br are normal the flies will differ from normal forms in the one character alone, *viz.*, vermilion. The dotted line below includes V, f and Br, hence the males receiving this chromosome are furrowed bar. Referring to the table showing the cross between a vermilion bar female with a furrowed male we see that there were 28 vermilion and 15 furrowed bar flies. Reading from the left again and omitting the normal allelomorphs, the upper dash line includes vermilion and furrowed and the lower dash line includes bar alone. The table shows that there were only three vermilion furrowed and six bar males, hence the interchange of material between vermilion and furrowed took place less frequently than it did between furrowed and bar. Since the per cent. of crossing over between any two genes is taken as the index of the relative distance between those genes, then furrowed lies much closer to vermilion than it does to bar.

The fine lines represent double crossing over, of which no representatives were found in this cross.

SUMMARY AND CONCLUSIONS

Crosses were made with mutant stocks of *Drosophila* with wild stock from many localities in the United States, from the West Indies, France and Australia in order to discover, if possible, if hybridization is an essential factor in the formation of mutant races. From 16,637 flies of the F_2 generation seven flies arose which varied from the normal type and which bred true. If we discard the four with the character "tau" for reasons given above, then the result is narrowed to three flies with two characters. This gives one mutant to every 5,545 flies. Therefore, a mutation has occurred so seldom that we can scarcely attribute hybridization as its cause. It is highly probable that if the same number of wild flies had been reared under

favorable conditions for the survival of any new forms that appeared just as many mutations would have been found as in the above experiment. In the light of these results we can attribute the origin of mutations only to chance, since hybridization as a causal agent does not occupy a privileged position relative to the effect.

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LINKAGE AND SEMI-STERILITY

THE Florida velvet bean (*Stizolobium deeringianum*) has normal pollen and embryo-sacs; it flowers (when sown in May) early in September; and has pigmented (mottled) seed-coats. The Yokohama bean (*Stizolobium hassjoo*) has also normal pollen and embryo-sacs; it flowers in July; and has its seed-coats unpigmented. The first-generation hybrids of Florida by Yokohama had half their pollen and embryo-sacs aborted (1, 2); flowered at the end of August; and had more or less pigmented seed-coats. In the second generation, half of the plants had normal pollen and embryo-sacs, and half showed semi-sterility (1, 2). These plants flowered from July to September, the majority being late. About three-quarters had pigmented seed-coats; and one-quarter, colorless seed-coats.

Most of the semi-sterile plants, and also most of the plants with pigmented seed-coats, were late in flowering. The semi-sterile plants, however, were not later than the fertile, in the second generation of the *Florida by China* cross. Hence there is no necessary connection between semi-sterility and lateness. A random sample of five second-generation plants of the Florida by Yokohama cross gave one family with pigmented seed-coats, one family with colorless seed-coats, and three families segregating into pigmented and colorless in about the ratio 3:1. Hence the pigmentation of the seed-coat is not a mere physiological consequence of lateness, but is determined by a definite factor. If K is the factor from the Florida concerned with semi-sterility; P , a factor concerned with pigmentation of seed-coat; and H , the main factor for lateness; then K and H are strongly coupled in the gametes of the first-generation plants, as are also P and H . K and P show secondary coupling.